

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
OXYNA PALPALIS (COQUILLET) (DIPTERA: TEPHRITIDAE) ON
ARTEMISIA TRIDENTATA NUTTALL (ASTERACEAE)
IN SOUTHERN CALIFORNIA**

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Abstract.—*Oxyyna palpalis* (Coquillett) is a univoltine, circumnatal tephritid uniquely reproducing as an inquiline in rosette galls of *Rhopalomyia florella* Gagné (Diptera: Cecidomyiidae) of terminal buds on branches of *Artemisia tridentata* Nuttall. Its larvae also routinely function as facultative predators of *R. florella* larvae, novel behavior for Tephritidae. The egg, first-, second-, and third-instar larvae, and puparia are described and figured for the first time. The egg is distinguished by a pedicel circumscribed by one complete and a partial second ring of irregularly shaped micropyles. All three larval instars of *O. palpalis* are compared to and distinguished from those of *O. aterrima* (Doane), its only other known congener in North America. Oviposition occurs in spring (June) in southern California in nearly fully formed galls of *R. florella* containing young larvae of this cecidomyiid. The young larvae of *O. palpalis* pass the summer (June–September) as first instars singly in small, central, ovoidal cells basad of the cecidomyiid larvae. Second instars occupy their still-small, separate chambers until late fall/early winter (September–October), when some begin to molt to third instars. By mid-winter (February) all larvae are third instars, which continue to overwinter and grow slowly until the resumption of the spring flush of new plant growth (March). At this time, one to six or more third instars enlarge the central gall chamber to accommodate their faster growth and feed gregariously. Cecidomyiid larvae encountered during this third stadium are killed and devoured; surviving immature gall midges usually occupy the periphery of the galls. Pupariation follows in early April, and adults emerge by mid-April. *Eurytoma* sp. (Hymenoptera: Eurytomidae) and *Eupelmus* sp. (Hymenoptera: Eupelmidae) were individually reared from puparia of *O. palpalis* as primary, solitary, probably larval-pupal endoparasitoids. *Lycus* sp. (Hymenoptera: Pteromalidae) was reared from individual puparia as a gregarious, primary endoparasitoid.

Key Words: Insecta, *Oxyyna*, Asteraceae, *Artemisia*, nonfrugivorous Tephritidae, *Rhopalomyia*, Cecidomyiidae, biology, taxonomy of immature stages, galls, inquiline, circumnatal life cycle, parasitoids, insect predation

Oxyyna palpalis (Coquillett) (Diptera: Tephritidae) is one of two species of *Oxyyna* now known from North America (Foote et al. 1993, Goeden 2002b). The other species,

O. aterrima (Doane) was reviewed by Foote et al. (1993) and studied by Goeden (2002b), who synonymized it with *O. utahensis* Quisenberry.

MATERIALS AND METHODS

The present study was based in large part on dissections of samples of galls of the gall midge, *Rhopalomyia florella* Gagné (Diptera: Cecidomyiidae), on *Artemisia tridentata* Nuttall prob. ssp. *parishii* (A. Gray) H. M. Hall and Clements (Asteraceae) collected mainly 0.2 km north of the hamlet of Mile High and just south of the hamlet of Largo Vista; 1580-m elevation; Township 4N, Range 9W, Section 4; Angeles National Forest, Los Angeles Co., during 1996 and 1997. Excised *R. florella* galls, containing eggs and early-instar larvae of *O. palpalis*, and later, overwintered galls containing third instars and puparia of *O. palpalis* were sampled mid-monthly from gall-bearing plants during 1996 and 1997. Samples were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Eight eggs, 18 first-, seven second-, and 19 third-instar larvae and nine puparia dissected from galls were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional prepuparia and puparia in excised, opened galls were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Central Facility for Advanced Microscopy and Microanalysis, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reser-

voir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages mainly were used for studies of longevity in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Two pairs of virgin flies, each consisting of a male and a female obtained from emergence cages also were held in a clear-plastic, petri dish provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993); cecidomyiid names and gall terminology follow Gagné (1989). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001, 2002a, b), Goeden and Norrbom (2001), Goeden and Teerink (1999), and earlier works cited therein. Means \pm SE are used throughout this paper. All remaining voucher specimens and reared parasitoids of this tephritid reside in my research collections. Digital photographs used to construct text figures were processed with Adobe Photoshop® Version 6.

RESULTS AND DISCUSSION

Adult.—*Oxyina palpalis* originally was described as a *Tephritis* by Coquillett in Baker (1904) from a single male specimen from Ormsby County, Nevada. Quisenberry (1949) in his revision of *Oxyina* redescribed this species from three females and two males variously from California, Idaho, and Nevada. Foote and Blanc (1963) and Foote et al. (1993) pictured the right wing.

Immature stages.—The egg, first-, second-, and third-instar larvae, and puparium of *O. palpalis* are described below.

Egg: Thirteen eggs of *O. palpalis* dissected from field-collected galls of *R. florella* galls also bearing cecidomyiid larvae were white, opaque, smooth, ellipsoidal,

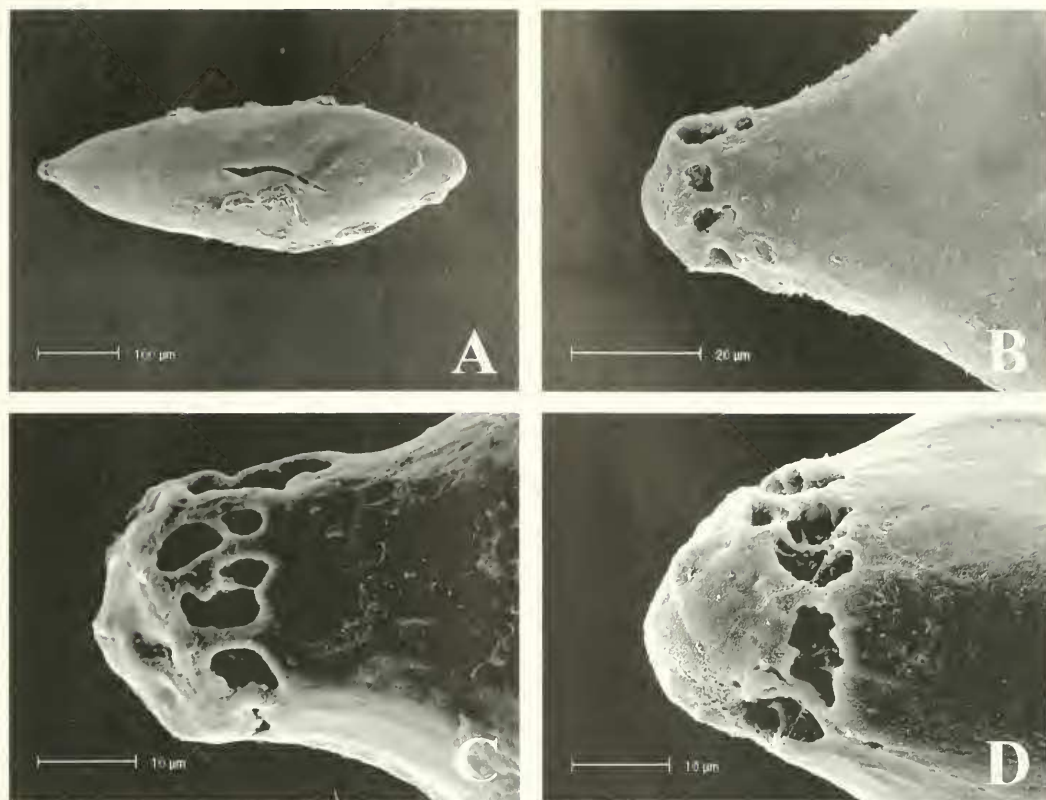


Fig. 1. Egg of *Oxya palpalis*: (A) habitus, anterior to left; (B) pedicel 1, (C) pedicel 2, (D) pedicel 3. (The three pedicels show variation in size, shape, and placement of micropyles.)

0.65 ± 0.02 (range, 0.62–0.68) mm long, 0.20 ± 0.00 (range, 0.20–0.20) mm wide, smoothly rounded at basal end, with a 0.2-mm, buttonlike pedicel at anterior end (Fig. 1A). The pedicel was circumscribed subapically by one complete and a partial second ring of irregularly shaped micropyles (Fig. 1B, C, D)

This is the first *Oxya* egg pictured at high magnification (Goeden 2002b). On average, the egg of *O. palpalis* is slightly longer and slightly narrower than that of *O. aterritima* (Goeden 2002b).

First instar larva: White, ellipsoidal, flattened anteriorly and posteriorly (Fig. 2A); body segments with hemispherical or posteriorly-directed, short-spinose, minute acanthae on intersegmental areas of metathorax and abdominal segments A1 through A6 as well as pleura and lateroventrum of

A1 through A6; prothorax and gnathocephalon smooth, the latter conical (Fig. 2B), both circumscribed by verruciform sensilla (Figs. 2B-1, -2); dorsal sensory organ, well-defined, flat pad (Fig. 2C-1); anterior sensory lobe (Fig. 2C-2) bears terminal sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4), supralateral sensory organ (Fig. 2C-5), and pit sensory organ (Fig. 2C-6); stomal sense organ reduced to two verruciform sensilla ventrolaterad of terminal sensory organ (Figs. 2C-7, D-1), not fused with flattened, protrudent, lateral integumental petal (Figs. 2C-8, D-2) above each mouthhook, one medial, papillate, integumental petal (Figs. 2C-9, D-3) between anterior sensory lobes and lateral integumental petals; mouthhook bidentate (Figs. 2B-3, C-10, D-4); median oral lobe laterally compressed, apically rounded (Figs. 2B-4,

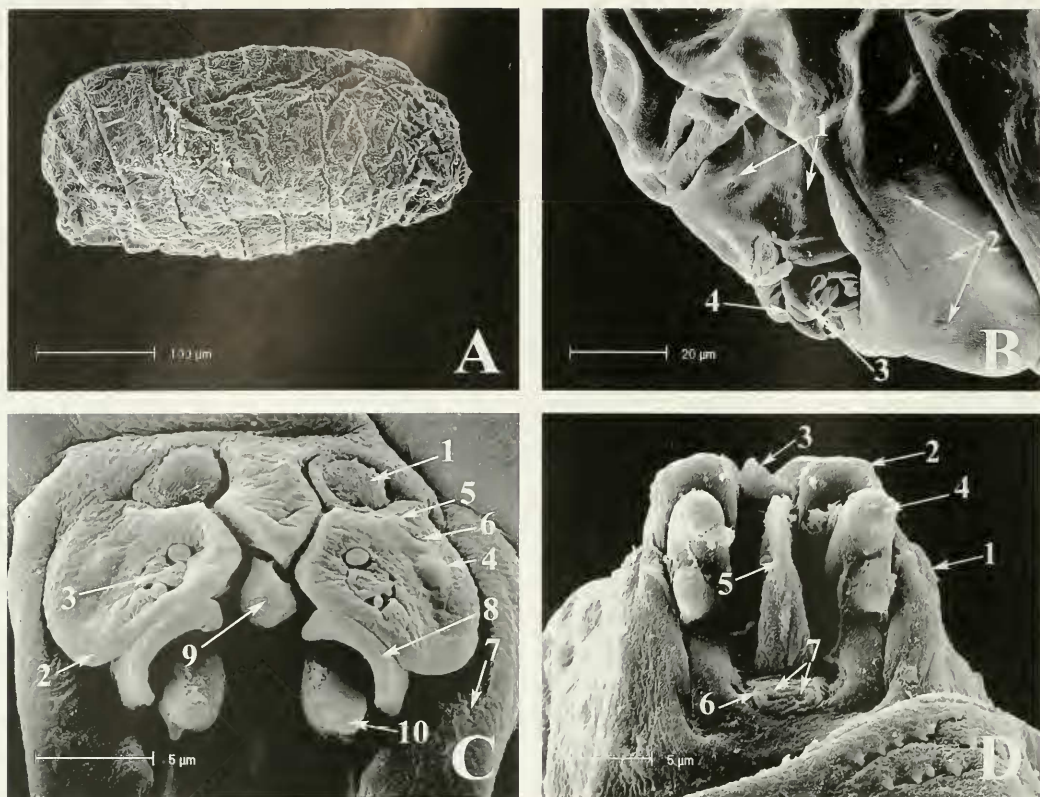


Fig. 2. First instar of *Oxyna palpalis*: (A) habitus, anterior to left. (B) gnathocephalon and prothorax, ventrolateral view, 1—verruciform sensilla on gnathocephalon, 2—verruciform sensilla on prothorax, 3—mouthhook, 4—median oral lobe; (C) gnathocephalon, frontal, close-up view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—stomal sense organ, 8—lateral integumental petal, 9—medial integumental petal, 10—mouthhook; (D) oral cavity, ventral view, 1—stomal sense organ, 2—lateral integumental petal, 3—medial integumental petal, 4—mouthhook, 5—median oral lobe, 6—labial lobe, 7—pores.

D-5); labial lobe (Fig. 2D-6) broad, separated from median oral lobe, and with two pores ventrally (Fig. 2D-7); anterior spiracle absent; lateral spiracular complexes not seen; caudal segment (Fig. 3A) with a stelex sensillum dorsolaterad (Fig. 3A-1), laterad (Figs 3A-2, B), and ventrolaterad (Figs. 3A-3, C-1) of posterior spiracular plate (Figs. 3A-4, D); posterior spiracular plate bears two rimae (Fig. 3D-1), ca. 0.005 mm long, and four, unbranched or bifurcate, spinose or apically toothed (some bifurcate) interspiracular processes (Fig. 3D-2), the longest process measuring 0.007 mm; intermediate sensory complex (Figs. 3A-5, C-

2, D-3) consists of stelex sensillum (Fig. 3C-3) and medusoid sensillum (Fig. 3C-4).

The habitus of the first instar of *O. palpalis* is similar to the first instar of *O. aterrima*; however, as with *Trupanea* spp. (Goeden and Teerink 1999), *Neaspilota* spp. (Goeden 2001), and *Tephritis* spp. (Goeden 2002a), the incidence and patterns of minute acanthae on the thorax and abdomen show interspecific differences. *Oxyna palpalis* has fewer minute acanthae in the intersegmental areas of the thorax and abdominal segments A1 and A2, and unlike *O. aterrima*, none on or between abdominal segments A3 through A6 (Goeden 2002b).

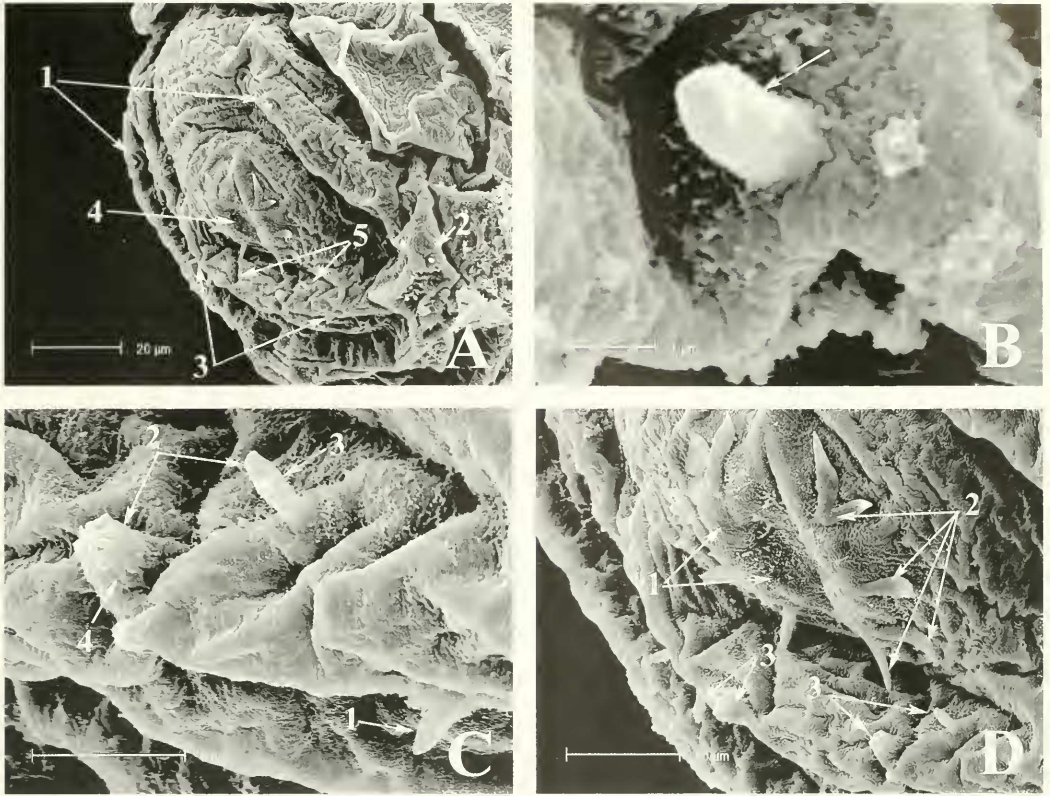


Fig. 3. First instar of *Oxyna palpalis*, continued; (A) caudal segment, 1—dorsolateral stelex sensilla, 2—lateral verruciform sensillum, 3—ventrolateral stelex sensillum, 4—posterior spiracular plate, 5—intermediate sensory complexes; (B) lateral stelex sensillum (arrow); (C) 1—ventrolateral verruciform sensillum, 2—intermediate sensory complex (composed of), 3—stelex sensillum, 4—medusoid sensillum; (D) posterior spiracular plate with 1—two rimae, 2—four interspiracular processes, and 3—two intermediate sensory complexes.

The first instar of *O. aterrima* has two, medial, integumental petals (Goeden 2002b); whereas, *O. palpalis* has only one (Figs. 2C-9, D-3). The single, lateral integumental petal above each mouthhook is fused with the stomal sense organ in *O. aterrima* (Goeden 2002b), but they are not fused in *O. palpalis* (Figs. 2C-8, D-2). The mouthhooks are tridentate in the first instar of *O. aterrima* (Goeden 2002b), but are bidentate in *O. palpalis* (Figs. 2B-3, C-10, D-4). The lateral sensilla surrounding the posterior spiracular plate of *O. aterrima* are verruciform (Goeden 2002b); whereas, these are stelex sensilla in *O. palpalis* (Figs 3A-2, B). The interspiracular processes on the caudal segment of *O. aterrima* are unbranched (Goeden 2002b); whereas, some

processes of *O. palpalis* are two-branched (Fig. 3D-2).

Second instar larva: Ovoidal, rounded anteriorly, truncated posteriorly (Fig 4A), body segments with short-spinose, posteriorly-directed, minute acanthae (Fig. 4B-1) circumscribing intersegmental areas of thorax and abdomen; thorax and gnathocephalon smooth (Fig. 4B), the latter conical, the former circumscribed around middle with verruciform sensilla (Fig. 4B-1); dorsal sensory organ, a well-defined, flat pad (Figs. 4C-1, D-1); anterior sensory lobe (Fig. 4C-2) with terminal sensory organ (Fig. 4C-3), lateral sensory organ (Fig. 4C-4), supralateral sensory organ (Fig. 4C-5), and pit sensory organ (Fig. 4C-6); two pairs of foliose, protrudent, lateral integumental

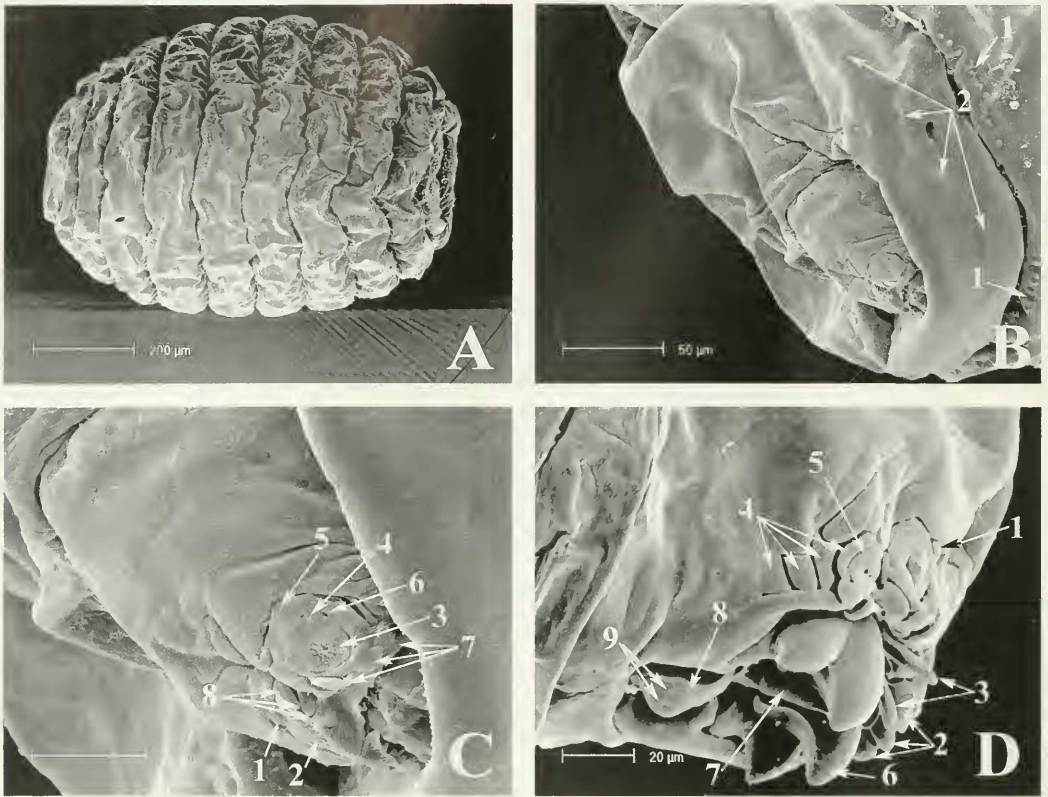


Fig. 4. Second instar of *Oxyna palpalis*: (A) habitus, anterior to left; (B) prothorax and gnathocephalon, frontolateral view, 1—minute acanthae, 2—verruciform sensillum; (C) gnathocephalon, frontolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—lateral integumental petals, 8—medial integumental petals; (D) gnathocephalon, ventrolateral view, 1—dorsal sensory organ, 2—lateral integumental petals, 3—ventral, medial integumental petals, 4—oral ridges, 5—stomal sense organ, 6—mouthhook, 7—median oral lobe, 8—labial lobe, 9—pores.

petals (Figs 4C-7, D-2) above each mouthhook, two pairs of papillate, medial integumental petals (Fig. 4C-8) between each anterior sensory organ, the ventral pair elongate (Fig. 4D-3); at least four oral ridges (Fig. 4D-4) ventrolaterad of each anterior sensory lobe and stomal sense organ (Fig. 4D-5); mouthhook (Fig. 4D-6) with two teeth; median oral lobe laterally flattened (Fig. 4D-7); labial lobe (Fig. 4D-8) broad, separated from median oral lobe, with two pores ventrally (Fig. 4D-9); anterior thoracic spiracle (Fig. 5A) with five, rounded, wedge-shaped papillae; lateral spiracular complexes not seen; caudal segment (Fig. 5B)

(Figs. 5B-1), laterad (Fig. 5B-2), and ventrolaterad (Figs. 5B-3, C-1) of posterior spiracular plate (Figs. 5B-4, D); posterior spiracular plate with four, elongate, upright, foliose, interspiracular processes (Fig. 5D-1), the longest process measuring 0.011 mm; intermediate sensory complex (Figs. 5B-5, C-2) consists of stelex sensillum (Fig. 5C-3) and medusoid sensillum (Fig. 5C-4).

One major difference between the second instars of *O. palpalis* and *O. aterrima* is the absence of a black marking on the abdominal ventrum of the former species, where the ventrum and pleura of the latter species are densely covered with knoblike minute acanthae (Goeden 2002b). In *O. palpalis*

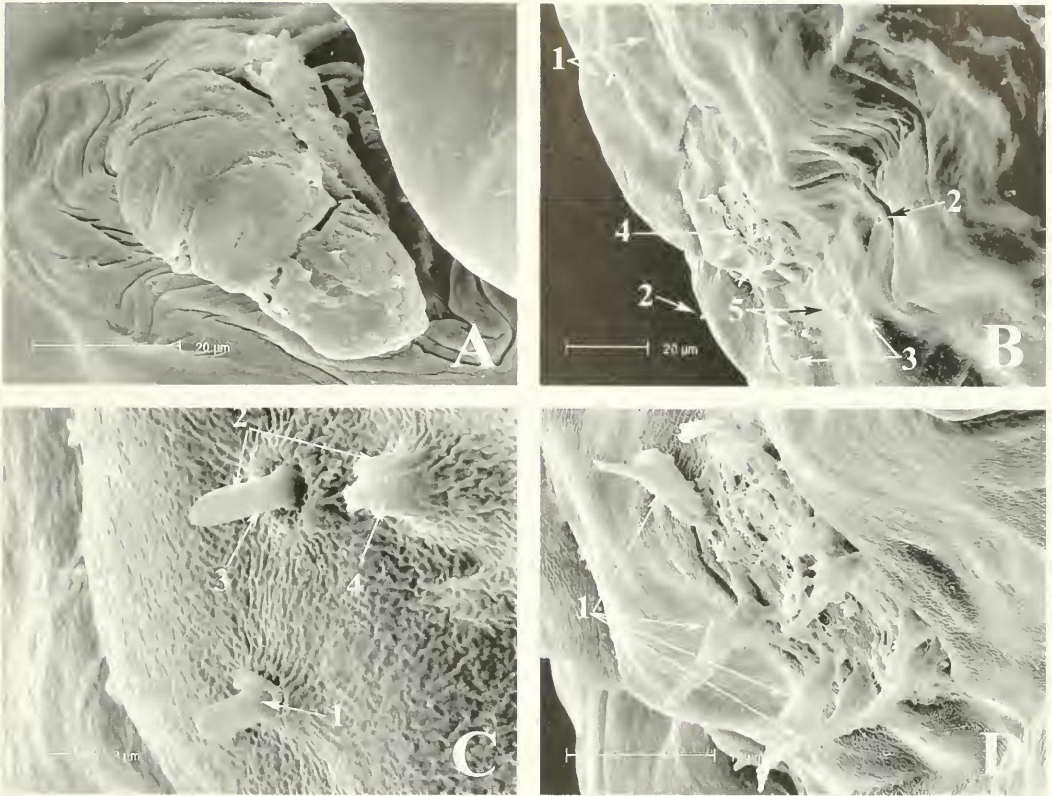


Fig. 5. Second instar of *Oxya palpalis*, continued: (A) anterior spiracle; (B) caudal segment; caudal segment, 1—dorsolateral stalex sensilla, 2—lateral stalex sensilla, 3—ventrolateral stalex sensilla, 4—posterior spiracular plate, 5—intermediate sensory complexes; (C) 1—ventrolateral stalex sensillum, 2—intermediate sensory complex (composed of), 3—stalex sensillum, 4—medusoid sensillum; (D) posterior spiracular plate, 1—four interspiracular processes.

the minute acanthae are short-spinose and confined mainly to the intersegmental areas of the thorax and abdomen. *Oxya palpalis* has two pairs of medial integumental petals between each anterior sensory lobe (Fig. 4C-8); whereas, *O. aterrima* has only one such pair (Goeden 2002b). The inner, ventral oral ridge among the four such ridges of *O. aterrima* is ventrally toothed and fused with the stomal sense organ (Goeden 2002b); whereas, none of the four oral ridges of *O. palpalis* is toothed nor fused with the stomal sense organ (Figs. 4D-3, 4).

Third instar larva: Pale yellow or white, ovoidal, tapering anteriorly, truncated posteriorly, distinctly segmented (Fig. 6A), short-spinose, posteriorly-directed, minute acanthae in transverse bands on dorsopos-

terior fifth of gnathocephalon (Figs. 6A, B-1), minute acanthae also circumscribe anterior fourth of thoracic segments and anterior fourth of abdominal segment A1, dorsum, ventrum and anterior third of pleura of A2-A7, and all but posterior of spiracular plate A-8 (Fig. 7D-1); gnathocephalon smooth, conical (Fig. 6B); dorsal sensory organ well-defined, hemispherical (Figs. 6B-2, C-1); anterior sensory lobe bears terminal sensory organ (Figs. 6B-3, C-2), lateral sensory organ (Fig. 6C-3), supralateral sensory organ (Fig. 6C-4), and pit sensory organ (Fig. 6C-5); nine or 10 oral ridges (Fig. 6D-1) laterad and ventrolaterad of anterior sensory lobe and stomal sense organ, at least six lobes ventrally toothed and separate from prominent stomal sense organ

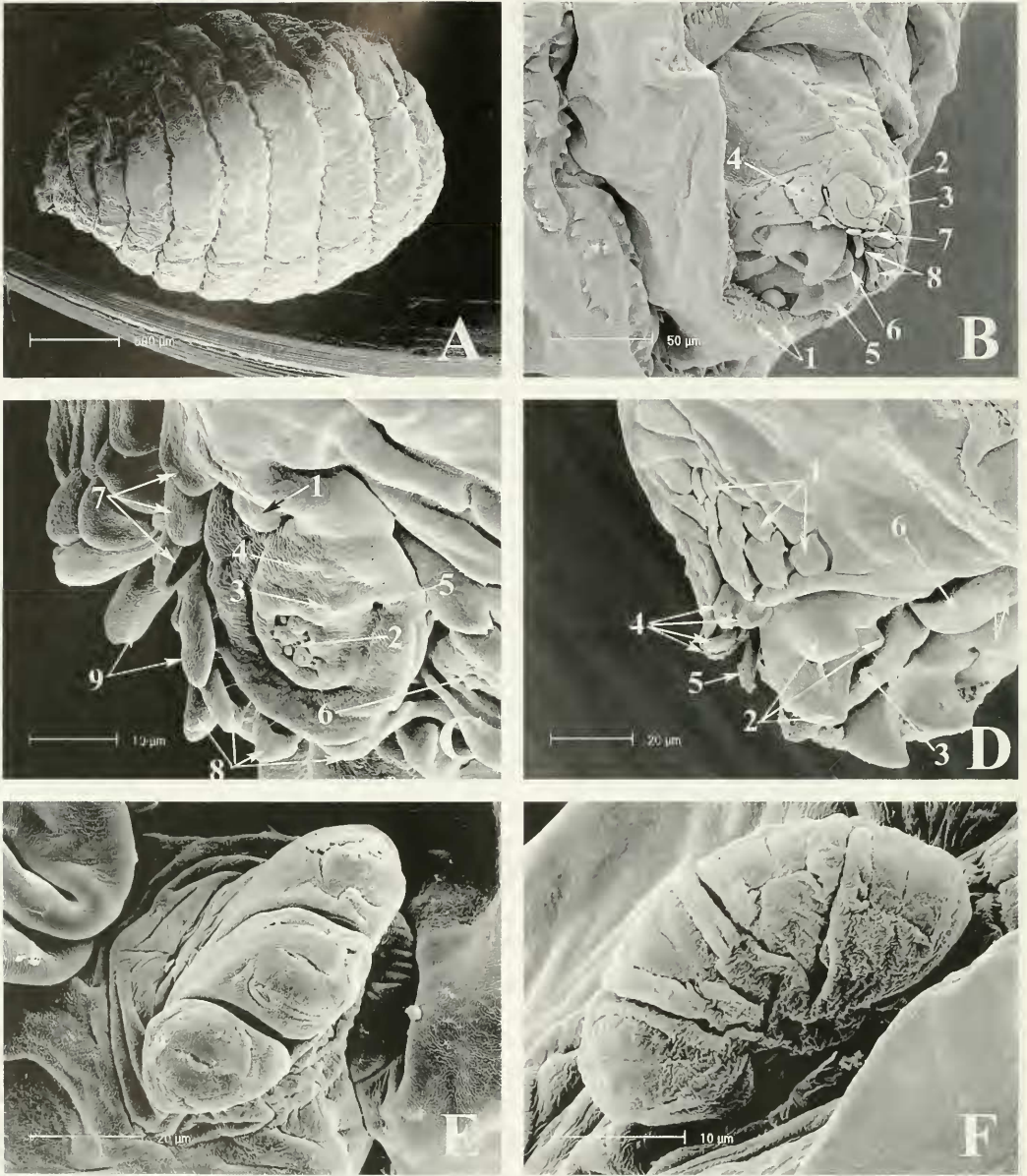


Fig. 6. Third instar of *Oxya palpalis*: (A) habitus, anterior to left; (B) gnathocephalon, ventrolateral view, 1—minute acanthae, 2—dorsal sensory organ, 3—terminal sensory organ, 4—stomal sense organ, 5—mouthhook, 6—median oral lobe, 7—lateral integumental petal, 8—inner, lateral integumental petals; (C) gnathocephalon, dorsolateral view, 1—dorsal sensory organ, 2—terminal sensory organ, 3—lateral sensory organ, 4—supralateral sensory organ, 5—pit sensory organ, 6—stomal sense organ, 7—medial integumental petals, 8—lateral integumental petals, 9—inner, lateral integumental petals; (D) gnathocephalon and oral cavity, ventrolateral view, 1—oral ridges, 2—three-toothed mouthhook, 3—median oral lobe, 4—lateral integumental petals, 5—inner, lateral integumental petal, 6—labial lobe, 7—pores; (E) anterior spiracle with three papillae; (F) anterior spiracle with four papillae.

(Fig. 6B-4, C-6); mouthhook (Fig. 6B-5, D-2) tridentate (Fig. 5D-2); median oral lobe laterally flattened, apically rounded (Figs. 6B-6, D-3); three pairs of medial integumental petals in vertical row between anterior sensory lobes (Fig. 6C-7); five, lateral integumental petals between each mouthhook and anterior sensory lobe, including four foliose, lateral petals (Fig. 6B-7, C-8, D-4) and single, inner, elongate, papillate, lateral petal (Figs. 6B-8, C-9, D-5); labial lobe (Fig. 6D-6) broad, separated from median oral lobe, and with two pores ventrally (Fig. 6D-8); anterior thoracic spiracle with three (Fig. 6E, 7A-1) or four, rounded, wedge-shaped papillae (Fig. 6F); lateral spiracular complex of mesothorax with closed, relict spiracle (Fig. 7A-2) and six verruciform sensilla (Figs. 7A-3) in vertical row posteriorad of spiracle, additional verruciform sensillum posteriorad of fourth-most-vertical sensillum; lateral spiracular complex of metathorax similarly composed of closed, relict spiracle (Figs. 7A-4, B-1) and four verruciform sensilla (Figs. 7A-5, B-2) similarly positioned; lateral spiracular complex of first abdominal segment composed of closed, presumably relict spiracle (Figs. 7A-6, C-1) and three verruciform sensilla (Figs. 7A-7, C-2) similarly positioned; posterior spiracular plate (Figs. 7D-1, 8A) bears three, broadly elliptical rimae (Fig. 8A-1), ca. 0.03 mm long, and four, unbranched, spiniform, interspiracular processes (Fig. 8A-2), each ca. 0.007 mm long; stelex sensilla dorsolaterad (Figs. 7D-2, 8B), verruciform sensilla laterad (Figs. 7D-3, 8C), and stelex sensilla ventrolaterad (Fig. 7D-4) of posterior spiracular plate; intermediate sensory complexes (Figs. 7D-5, 8D) consist of stelex sensillum (Fig. 8D-1) and medusoid sensillum (Fig. 8D-2).

Fortunately, the third instars of both species of *Oxyina* known from North America have now been described in considerable detail, facilitating comparison between them. For example, the minute acanthae on third instars of *O. aterrima* are fewer in number, occupy fewer body segments, and

form different patterns (Goeden 2002b) than the minute acanthae on *O. palpalis*. *Oxyina palpalis* has at least nine or 10 oral ridges (Fig. 6D-1), six of which have ventrally toothed margins; whereas, *O. aterrima* has only two oral ridges (Goeden 2002b). All five lateral integumental petals of third instar *O. aterrima* are papillate (Goeden 2002b); whereas, only one of the five lateral integumental petals of the third instar of *O. palpalis* is papillate, the rest are foliose (Figs. 6B-7, C-8, D-4). The lateral spiracular complex of the mesothorax of *O. aterrima* has four verruciform sensilla (Goeden 2002b); whereas, this same complex in *O. palpalis* has seven verruciform sensilla (Figs. 7A-3). Similarly, the lateral spiracular complex of the first abdominal segment of *O. aterrima* has four verruciform sensilla, two pairs in separate vertical rows, (Goeden 2002b); whereas, this same complex in *O. palpalis* has three, vertical, verruciform sensilla (Figs. 7A-7, C-2).

The caudal segments of third instars of these congeners also differ considerably. The dorsolateral, lateral, and ventrolateral sensilla surrounding the posterior spiracular plate of *O. aterrima* are all verruciform. The intermediate sensory complex of this species also uniquely consists of two verruciform sensilla, and this composition distinguishes *O. aterrima* from third instars of all other nonfrugivorous tephritids examined by my coworkers and me to date (Goeden 2002b). In *O. palpalis*, the dorsolateral and ventral lateral sensilla are stelex in form (Figs. 7D-2, -4E, 8B), and the intermediate sensory complex is comprised of a stelex sensillum (Fig. 8D-1) and a medusoid sensillum (Fig. 8D-2), like all other third instars described by us to date.

Differences noted between the first and second instars of *O. palpalis* include the usual acquisition of an anterior spiracle in the second instar, the increase in the number of lateral integumental petals from one to three, and the drastic change in shape of the interspiracular processes (Figs. 3D-2, 5D-1). Differences noted between the second

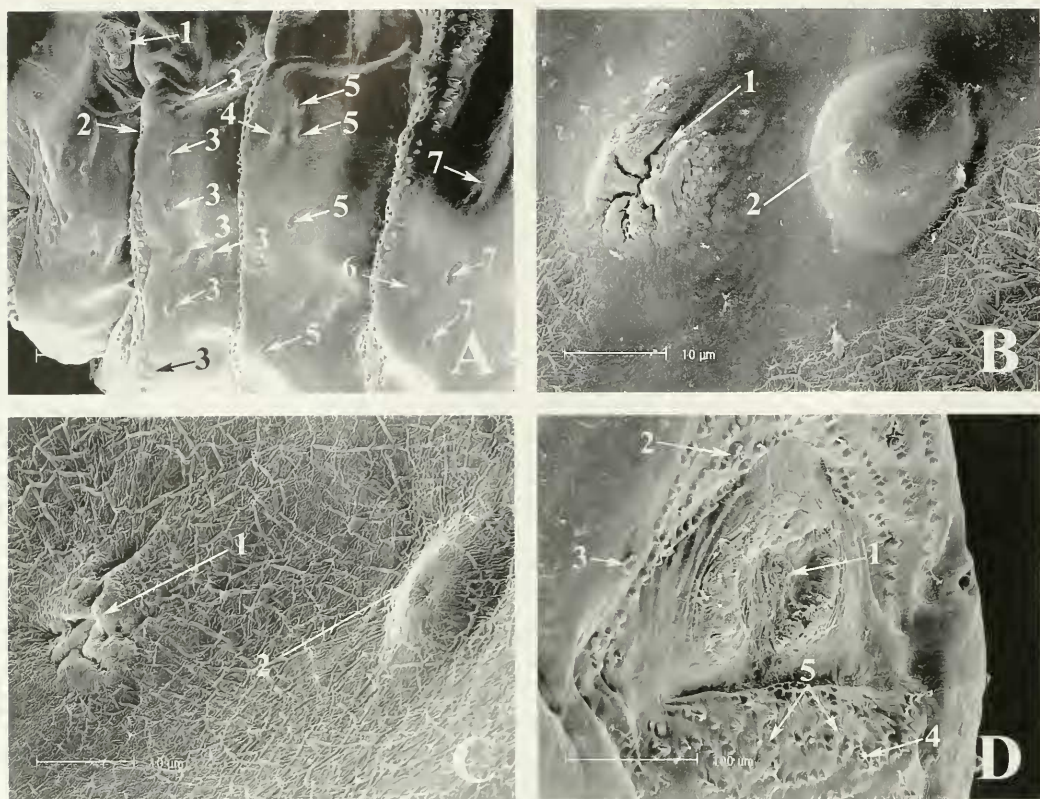


Fig. 7. Third instar of *Oxya palpalis*, continued: (A) lateral spiracular complexes, 1—anterior spiracle, 2—metathoracic spiracle, 3—verruciform sensillum, 4—mesothoracic spiracle, 5—verruciform sensillum, 6—first abdominal segment spiracle, 7—verruciform sensillum; (B) part of lateral spiracular complex of metathorax, 1—spiracle, 2—verruciform sensillum; (C) part of lateral spiracular complex of metathorax, 1—spiracle, 2—verruciform sensillum; (D) anal segment, 1—posterior spiracular plate, 2—dorsolateral stelex sensillum, 3—lateral verruciform sensillum, 4—ventrolateral stelex sensillum, 5—intermediate sensory complexes.

and third instars include a change in the incidence of the minute acanthae as described above. Other changes include increases from three (Fig. 4C-7) to five (Figs. 6B-7; B-8; C-9; D-4, -5) in the number of lateral integumental petals, which all are foliose in the second instar, but add a central, papillate petal in the third instar. Two pairs of medial integumental petals are present in the second instar (Fig. 4C-8); whereas, three pairs occur in the third instar (Fig. 6C-7). The anterior spiracles with five papillae in the second instar (Fig. 5A) compare with three (Figs. 6E, 7A-1) or four papillae (Fig. 6F) in the third instar. The sensilla surrounding the posterior spiracular plate are the same in number as in the second instar; however,

in the second instar the lateral sensilla are stelex (Fig. 5B-2), not verruciform, as in the third instar (Figs. 7D-3, 8C). The interspiracular processes on the posterior spiracular plate of the second instar are larger, foliose, and upright (Fig. 5D-1) compared to the small, resupinate, spiniform processes of the third instar (Fig. 8D-2).

Puparia: Reniform-ellipsoidal, light-, yellow-, or reddish-brown, rarely white (Fig. 9B), anterior end bears the invagination scar and anterior thoracic spiracles; caudal segment bears posterior spiracular plates (Fig. 9C), each with three broadly elliptical, raised rimae (Fig. 9C-1) and four, interspiracular processes (Fig. 9C-2). One hundred and five puparia averaged $3.04 \pm$



Fig. 8. Third instar of *Oxya palpalis*, continued: (A) posterior spiracular plate, 1—three rimae, 2—four interspiracular processes, (B) dorsolateral stelex sensillum, (C) lateral verruciform sensillum, (D) intermediate sensory complex, 1—stelex sensillum, 2—medusoid sensillum, 3—minute acanthae.

0.03 (range, 2.13–3.70) mm in length; 1.60 ± 0.016 (range, 1.14–1.99) mm in width.

DISTRIBUTION AND HOSTS

Oxya palpalis uniquely reproduces as an inquiline in the rosette galls of *Rhopalomyia florella* of terminal buds on branches of *Artemisia tridentata* in southern California. In this capacity it also functions as a facultative predator on the larvae and pupae of *R. florella* (see below), which also renders this tephritid rare and fascinating in the annals of tephritidology. Novak et al. (1967) reported that the larvae form small, succulent, polythalamous galls on small branches of *A. tridentata* in Idaho, but as documented in the next section of this paper, this interpretation was incorrect, as *O. palpalis* is not a gall-former. Foote et al. (1993) mapped the distribution of *O. pal-*

palis to include California, Idaho, Nevada, Oregon, Utah, Washington, and Wyoming. Thus, like that of *O. aterrima* (Goeden 2001b), the distribution of *O. palpalis* may coincide wholly with *A. tridentata sensu lato*, or in part with one or more of its subspecies (Hickman 1993). This is a shrub that inhabits dry soils, valleys, slopes from 300 to 3000+ m in the western U.S., i.e., north to Washington, the North Central States and south to New Mexico (Hickman 1993). The distribution of *A. tridentata* also extends into southwestern Canada (Barkley 1986).

BIOLOGY

Egg.—In each of 31, nearly fully formed rosette galls of *Rhopalomyia florella* (Gagne 1989) already containing larvae of this cecidomyiid (Fig. 10A), most of 51 eggs of

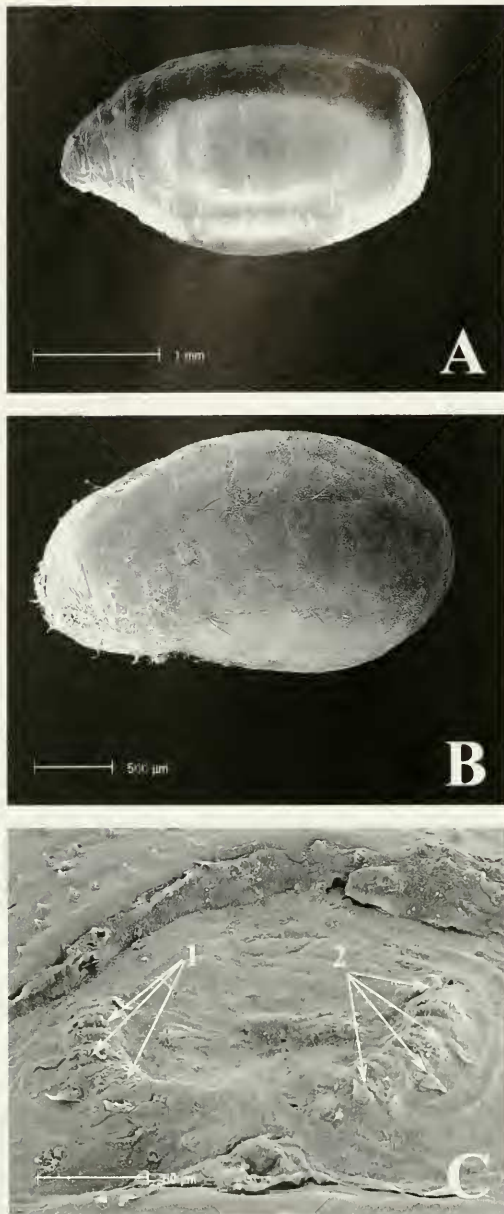


Fig. 9. *Oxyina palpalis*. (A) prepuparium, habitus, anterior to left; (B) puparium, habitus, anterior to left; (C) posterior spiracular plate, 1—three rimae, 2—four interspiracular processes.

O. palpalis were found inserted separately, a few in small clusters, pedicel-last, in leaf bases to depths of half to all of the egg lengths (Fig. 10B). Leaves at the margins or in the centers of the galls received the

most oviposition, but a few eggs were laid upon, but not penetrating the tissues between adjacent bases of inner or outer leaves. About half of the eggs lay with their long axes parallel to the long axes of the galls (Fig. 10B); the remainder lay at angles of 5° to 45° to the long axes. Oviposition in galls was scattered throughout a stand of *A. tridentata*, like and sympatric with the galls of *R. florella*, and not confined to certain individual host-plants galled repeatedly over successive years (Headrick and Goeden 1998). This is similar to the pattern of the incidence of galls of *O. aterrima* (Goeden 2002b). Some galls bore tephritid eggs on opposite sides that showed different degrees of embryony, presumably indicative of oviposition by different females at different times. An average of 3.4 ± 0.4 (range, 1–10) eggs was found in these 31 galls. Galls containing eggs of *O. palpalis* (Fig. 10A) averaged 6.3 ± 0.4 (range, 4.3–11.5) mm in length, and 4.0 ± 0.2 (range, 0.6–6.8) mm in width. The linear leaves investing these galls averaged 3.5 ± 0.3 (range, 2.0–8.6) mm in length and 0.9 ± 0.04 (range, 0.6–1.3) mm in width.

Larva.—Upon eclosion, most first instars of *O. palpalis* tunneled into the center of the gall basad of the young, cecidomyiid larvae and leaf bases (Fig. 10C), where each first instar remained for up to 3 months within an individual, ovoidal, open, smooth-walled cell. An average of 2.3 ± 0.2 (range, 1–5) first instars of *O. palpalis* were found in a total of 53 infested galls sampled monthly during the first 3 months following oviposition, during which time the subspheroidal (smaller) (Fig. 10A) to hemispheroidal (larger) galls averaged 6.9 ± 0.3 (range, 3.1–11.5) mm in length and 4.8 ± 0.2 (range, 2.9–7.4) mm in width. The linear leaves laterally surrounding the galls averaged 4.4 ± 0.2 (range, 1.4–8.6) mm in length and 0.9 ± 0.03 (range, 0.6–1.4) mm in width. Seventy-three ovoidal to spheroidal cells containing the first instars of *O. palpalis* averaged 0.78 ± 0.09 (range, 0.28–4.6) mm in length and 0.48 ± 0.18

(range, 0.21–0.99) mm in width. The size of most of these cells containing first instars slowly increased during the first stadium. Unfortunately, the number of cecidomyiid larvae was not recorded in most galls; however, 14 galls containing first instars of *O. palpalis* also were noted to contain an average of 2.2 ± 0.5 (range, 1–8) larvae of *R. florella*. Also, it was subsequently noted that most galls of *R. florella* without *O. palpalis* contained only a single, centrally located larva (Fig. 11D). Thus, some galls containing first instars of *O. palpalis* also contained dead, centrally located, cecidomyiid larva(e) presumably killed after accidental contact with a tephritid larva. Indeed, at least for later instars of *O. palpalis* in those many galls found to be lacking *R. florella* (see below), this relationship may represent nutritionally advantageous, facultative predation.

The larva next molted to the second instar (Fig. 10D), evidenced as the cast cephalopharyngeal skeleton remaining in the cell. This instar may also last about 3 months and is one stage found in overwintering galls in southern California (see below). The external dimensions of 28 galls found to contain second instars measured 6.8 ± 0.3 (range, 3.7–11.4) mm in length by 5.7 ± 0.3 (range, 2.9–8.6) mm in width. The linear leaves investing these galls averaged 4.6 ± 0.3 (range, 1.7–9.1) mm in length and 1.1 ± 0.04 (range, 0.7–1.7) mm in width. These 28 galls each contained an average of 1.8 ± 0.2 (range, 1–6) second instars of *O. palpalis* (Fig. 10D). Two of these galls (7%) contained two and three larvae clustered together in a central, common, open cavity. The remaining 26 galls contained one or more second instars in separate, open, ovoidal cells (Fig. 10D) that averaged 1.3 ± 0.06 (range, 0.6–2.0) mm in length and 0.8 ± 0.04 (range, 0.4–1.1) mm in width. Thus, the galls grew little on average during the second stadium, as did the cells containing individual second instars of *O. palpalis* (Fig. 10D). Ten galls were recorded to contain dead larvae of *R.*

florella or none, the latter of which was presumed to reflect complete consumption by *O. palpalis*, but again, cecidomyiid incidence was not recorded in another 10 of these galls, so the incidence of cecidomyiid mortality may actually have been higher.

Oxyna palpalis also overwinters as third instars in southern California (Figs. 10E, F). This is the stage during which the greatest amount of larval growth and attendant increase in gall cavity size takes place (Figs. 10E, F). Seventy-eight galls containing third instars of *O. palpalis* averaged 8.9 ± 0.2 (range, 5.1–13) mm in length by 7.4 ± 0.2 (range, 2.1–4.5) mm. The linear leaves laterally surrounding the galls averaged 5.3 ± 0.2 (range, 2.2–10.8) mm in length and 1.2 ± 0.03 (range, 0.9–1.7) mm in width. Thus, on average, galls increased little, if any, in size during the equally slow growth of the third instars during the winter through early spring, when in response to renewed plant growth following winter rainfall, the cavities that contained the third instars expanded to accommodate the fast-growing, *O. palpalis* larvae. The 65, frass-lined, ovoidal or irregularly shaped, centrally located, open cells that contained single instars of *O. palpalis* within these 78 galls averaged 2.6 ± 0.1 (range, 1.1–5.1) mm in longest measurement by 1.7 ± 0.1 (range, 0.57–2.9) mm in shortest measurement, or about twice as large as cells containing single second instars. Moreover, in galls containing two or more third instars (Figs. 10E, F) these central cavities averaged 3.3 ± 0.2 (range, 1.7–5.1) mm in longest length by 2.6 ± 0.2 (range, 0.85–4.6) mm in shortest width, or, again, more than twice as large on average than cavities containing single second instars, or those with single third instars, sometimes occupying much of the interior of smaller galls. All told, the 78 galls contained an average of 1.7 ± 0.1 (range, 1–5) third instars (Figs. 10E, F). The lateral thickness of the walls of these galls averaged 1.8 ± 0.6 (range, 1.1–2.9) mm, which afforded insufficient spatial protection from parasitoids (see be-

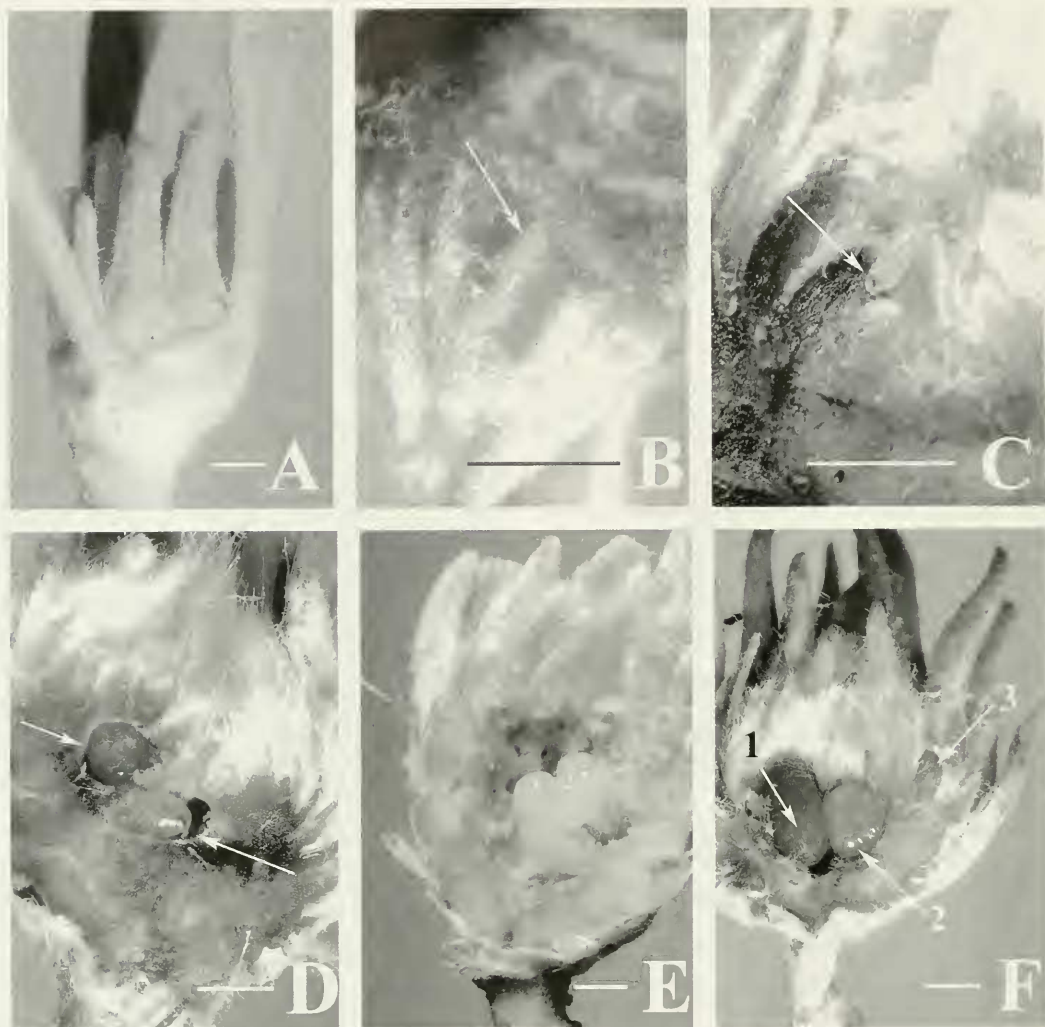


Fig. 10. Life stages of *Oxya palpalis* in galls of *Rhopalomyia florella*: (A) partly grown gall of *R. florella* that contained egg of *O. palpalis*, (B) egg of *O. palpalis* (arrow) in gall of *R. florella*, (C) newly eclosed, first instar of *O. palpalis* (arrow) tunneling into center of gall, (D) two, overwintering second instars of *O. palpalis* in separate chambers (arrows), (E) four third instars of *O. palpalis* in common, central cell in gall, (F) 1—newly formed puparium and 2—full-sized larva of *O. palpalis*, and 3—pupa of *R. florella* in same gall. Lines = 1 mm.

low) that attacked the third instars and puparia of *O. palpalis*. All told, third instars were found in samples over an 8-month period, 6 months into which, puparia first appeared in monthly gall samples.

Pupa.—Near the end of the third larval stadium, the third instar transformed into a prepuparium (Fig. 9A), which in *O. palpalis* was of relatively short duration. No window to facilitate future adult egress from the

galls was formed in the gall wall, unlike the windows made by *O. aterrima* third instars prior to prepupal formation (Goeden 2002b). The prepuparia of *O. palpalis* (Figs. 9A, 10F-2) transformed into puparia within the larval cells or among the cottony tomentum (Fig. 10F-1), which by then also contained pupae (Fig. 10F-3) or empty pupal exuviae of emerged, surviving *R. florella*, usually found on the periphery of a

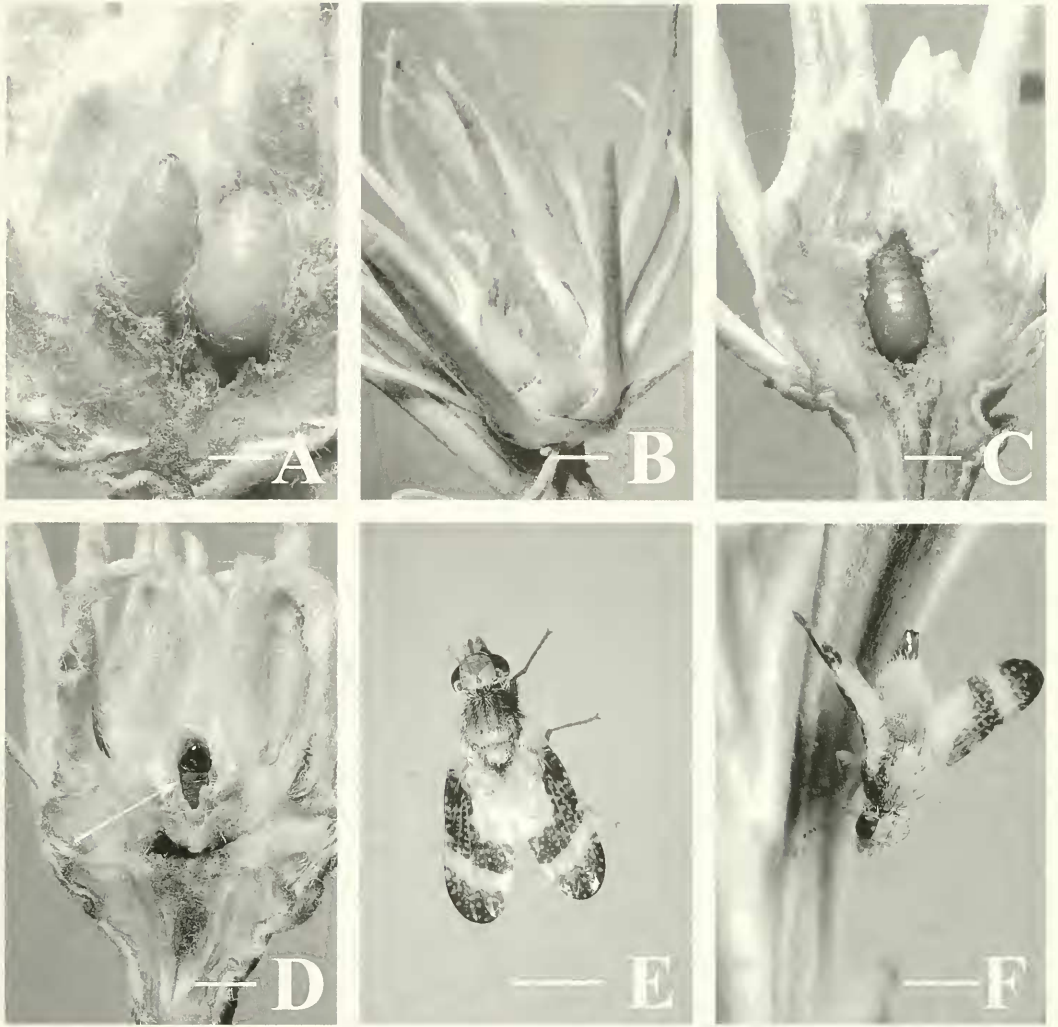


Fig. 11. Life stages of *Oxyna palpalis* in galls of *Rhopalomyia florella*, continued, (A) two puparia of *O. palpalis* in gall, (B) full-size gall that contained puparia of *O. palpalis*, (C) single central puparium of *O. palpalis* in gall, (D) single, central pupa of *R. florella* in gall, (E) male adult of *O. palpalis*, (F) female adult of *O. palpalis*. Lines = 1 mm.

gall (Fig. 10F-3). The anterior end of the puparium of *O. palpalis* usually faced distad, away from the base of the gall (Figs. 10F-1, 11). Eighty-four mature galls (Figs. 11B, C) sampled over a 2-mo period contained an average of 1.5 ± 0.1 (range, 1–5) puparia of *O. palpalis*. These galls externally averaged 9.1 ± 0.2 (range, 5.7–15.0) mm in length by 7.9 ± 0.2 (range, 5.0–11.4) mm in width. The linear leaves laterally surrounding the galls averaged 7.1 ± 0.3 (range, 2.6–16) mm in length and 1.4

± 0.03 (range, 0.8–2.5) mm in width. Sixty (71%) of the 84 galls each contained a frass-lined, ovoidal or irregularly shaped, central cavity that held a single puparium of *O. palpalis* (Fig. 11C), which averaged 3.4 ± 0.1 (range, 2.3–6.3) mm in longest measurement by 2.0 ± 0.1 (range, 1.1–3.4) mm in shortest measurement. Whereas, in galls containing two or more puparia (Fig. 11A) these central cavities averaged 4.1 ± 0.2 (range, 2.9–5.7) mm in longest length by 3.2 ± 0.1 (range, 2.3–4.6) mm in short-

Table 1. Incidence of *Oxya palpalis* in galls of *Rhopalomyia florella* on *Artemisia tridentata* on sample dates indicated.

Sample Date	<i>R. florella</i> Galls Sampled	
	No. Without <i>O. palpalis</i> (%)	No. With <i>O. palpalis</i> (%)
10.iv.1996	49 (84)	9 (16)
1.v. 1996	51 (84)	10 (16)
7.v. 1996	55 (79)	15 (21)
5.vi. 1996	?	15 (?)
18.vi. 1996	12 (38)	20 (62)
16.vii. 1996	15 (56)	12 (44)
13.viii. 1996	25 (71)	10 (29)
16.ix. 1996	76 (87)	11 (13)
16.x. 1996	35 (81)	8 (19)
13.xi.1996	60 (79)	16 (21)
18.xii. 1996	40 (70)	17 (30)
16.i. 1997	20 (71)	8 (29)
12.ii. 1997	34 (63)	20 (37)
13.iii. 1997	65 (81)	25 (19)
9.iv. 1997	76 (76)	24 (24)
16.iv. 1997	69 (78)	19 (22)
30.iv. 1997	45 (80)	11 (20)

est width, again, sometimes occupying much of the interior of smaller galls. The central location of a single pupa of *R. florella* in a gall without *O. palpalis* (Fig. 11D), when compared to a similarly located puparium of *O. palpalis* typical of the 60 galls containing single individuals noted above (Fig. 11C), most of which lacked any sign of *R. florella*, strongly suggests a high incidence of facultative, or at least accidental predation by the tephritid on the cecidomyiid. Table 1 records the incidence of *O. palpalis* in galls of *R. florella* on different sample dates.

Adult.—Adults exited galls presumably by pushing aside, between, and outward through the enfolding, apical, immature leaves and tomentum (Figs. 11A, C). Under insectary conditions, 17 males (Fig. 11E) lived an average of 48 ± 5 (range, 21–84) days, and 12 females (Fig. 11F) an average of 41 ± 6 (range, 12–75) days. These longevities are relatively long in duration for a circumnatal tephritid (Headrick and Goeden 1998). For example, males and females of

O. aterrima on average respectively lived half as long (Goeden 2002b).

Mating behavior.—The premating, mating, and postmating behaviors of *O. palpalis* were not studied in the field, nor were these behaviors observed in petri dish arenas of the type found to be so useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994, Goeden 2002b). In two such arenas, adults exhibited a few behaviors similar to *O. aterrima* (Goeden 2002b) and typical of other circumnatal, gallicolous species, cf., *Procecidochares*, previously studied in southern California, i.e., a lack of courtship behavior, the exhibition of enantion type wing movements by both sexes, and male stalking of females prior to mating (Goeden and Norrbom 2001; Headrick and Goeden 1994, 2000).

Seasonal history.—*Oxya palpalis* is a univoltine, circumnatal species (Headrick and Goeden 1994, 1998) reproducing in rosette galls of *Rhopalomyia florella* of terminal buds on branches of *A. tridentata* in southern California (Gagné 1989). Eggs are laid in nearly fully formed galls containing young larvae of *R. florella* in early summer (June) and *O. palpalis* passes the summer (June–September) as first instars. These larvae molt to the second instar beginning in mid-September in early fall, and to the third instar beginning in mid-October, initially overwintering as both second and third instars, but solely as third instars by mid-winter (February) of the following year. The third instars complete this instar beginning in early spring (March) at the time of the renewed flush of host-plant growth. Pupariation and adult emergence follow in April and the adults mate and probably oviposit in newly formed galls of *R. florella* on or near the same plants from which both species of flies emerged.

Natural enemies.—Many individual *Eurytoma* sp. (Hymenoptera: Eurytomidae) and six individuals of *Eupelmus* sp. (Hymenoptera: Eupelmidae) were reared separately from individual puparia as primary, soli-

tary, probably larval-pupal endoparasitoids. One, three, three, and seven individuals of *Lyrceus* sp. (Hymenoptera: Pteromalidae) were reared from individual puparia of *O. palpalis* as gregarious, primary endoparasitoids.

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